Title *Calluna vulgaris* canopy height in relation to carbon dioxide flux from heathland on blanket peat

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Abstract

This study seeks to address the proposition that the canopy height of *Calluna vulgaris* is a measure of the CO_2 balance of heathlands on ombrotrophic peatlands and thus can be used as an objective tool to define when to manage (typically by prescribed burning) heathlands. To test this idea a monthly dataset of CO_2 flux and associated environmental variables was gathered from three localities in the South Pennines and the Peak District National Park of northern England between 2007 and 2010, covering a range of *C. vulgaris* canopy heights. It was found that both gross fluxes of CO_2 (ecosystem respiration and photosynthesis) were modelled best by models incorporating a dependence on canopy height. Ecosystem respiration was positively correlated and photosynthesis was negatively correlated to canopy height. It was found that as canopy height increases, the amount of photosynthesis per unit respiration decreased. Despite the relationship between the gross fluxes and canopy height, models of net ecosystem exchange suggested that there was no canopy height at which blanket peat dominated by *C. vulgaris* would be a net annual sink of CO_2. This was due to the relatively deep water tables at the sites which served to enhance ecosystem respiration. As no transition between a net sink and source of CO_2

was observed it was not possible to make a recommendation as to what canopy height is optimal for management interventions to maximise carbon accumulation. As heathlands on blanket peat in the areas studied are predicted to be net sources of CO_2 to the atmosphere vegetation management away from *C. vulgaris* dominance is recommended to improve the biogeochemical functioning of these bogs.

Introduction

Heathlands dominated by *Calluna vulgaris* (L.) Hull (hereafter known as heather) are one of the most distinctive and characteristic habitats across large areas of the sub-montane zone of the United Kingdom (UK) and the Republic of Ireland. These areas are of significant cultural, aesthetic and economic value to the UK (Holden et al. 2007) and are internationally important biogeographically, given their rare occurrence outside of the British and Irish Isles (Thompson et al. 1995). Heathlands are semi-natural habitats which require management to prevent vegetative succession away from heather dominance. In the UK the management of upland heath is typically, but not exclusively, by prescribed burning at regular intervals, which when done well reinvigorates growth of the heather (Hobbs & Gimingham 1987).

Concerns have long been raised as to the environmental impact of prescribed heathland burning on organic soils, particularly peat (e.g. Imeson 1971). These concerns primarily centre around issues of biodiversity loss (Harris et al. 2011), reductions in carbon storage/soil erosion (e.g. Garnett et al. 2000) and deterioration of catchment-scale water quality (e.g. Yallop & Clutterbuck 2009). However, the debate about burning is increasingly moving away from a discussion of ‘to-burn or not-to-burn’ to a debate about when it is most appropriate/sustainable, from an environmental perspective, to burn heathland on differing soil types (Bain et al. 2011). This paper is specifically interested in heathland on top of ombrotrophic peat soils (as per the definition of Avery 1980), where issues of biodiversity, carbon storage and water quality (e.g. dissolved organic carbon losses) all coincide.

In the UK the timing of a prescribed burn is based on a balance between the need for taller heather to support game birds and the need to reduce wildfire risk. It is common for land managers to use a rotational period (i.e. a set interval of time between burns) to define when to burn. The median rotational interval in the UK is ~20 years (Yallop et al. 2006), with adjacent plots burned sequentially to create a 'mosaic' of stand-ages. A number of studies have examined contrasting rotational intervals in order to identify recommendations for best practice. From a biogeochemical perspective, Clay et al. (2010) found that burning on rotational periods less than 32 years would improve the C budget of North Pennine blanket peat relative to unburnt, heather dominated controls. Moreover, Allen et al. (2013) predict that burning on shorter rotations (~8 years) can reduce C losses from sites relative to longer rotational periods when wildfire return intervals are decreasing. However evidence from Yallop and Clutterbuck (2009) suggests decreasing rotational periods could increase dissolved organic carbon (DOC) export from peat covered catchments as the surface area of newly burned peat is positively correlated to surface water colour/DOC concentrations. As the rotational period shortens the amount of newly burned peat will increase as plots are being burned more regularly and this increase in the surface area of newly burned peat will increase export of DOC. However, it was argued by Holden et al. (2012) that it may not necessarily be burning *per se* that leads to increased DOC, but the removal of vegetation, as bare peat is associated with greater colour production than vegetated peat. A similar argument has also been made with reference to methane fluxes where burning has no apparent impact on methane uptake capacity on regularly burned (10 year cycle) blanket peat heath whereas complete heather removal (without burning) uniformly decreased methanotroph populations (Chen et al. 2008).

Despite their popularity it can be argued that using set rotational periods to define when to burn is essentially an arbitrary criterion. This is because heather growth rates are controlled by location-specific factors (soil type, climate, grazing etc. - Gimingham 1972) and thus there are no broadly applicable recommendations of when to manage heather based on rotational periods. To illustrate the point Mowforth and Sydes (1989) found that heather growth to a canopy height between 20-30 cm tall would take 6-10 years in southern England and 10-12 years in north-eastern Scotland, thus it would be impossible to recommend a single burn frequency that would suit both of them.

There is evidence that instead of burning at a fixed temporal interval it makes more objective sense to burn once the canopy reaches a certain height. Burch (2008) suggests that on wet heaths (e.g. heath on blanket peat) burning should be carried out when the canopy reaches 25 – 30 cm in order to maximise post-burn bryophyte regeneration and minimise the potential for a destructive 'hot' burn. A broader study of plant community dynamics by Harris et al. (2011) concurred with Burch (2008) in recommending burning at (or before) a canopy height 25 cm to prevent damage to species diversity. However, despite this ecological evidence for the benefit of using canopy height few biogeochemical studies of burning have considered canopy height explicitly, instead preferring to consider rotational period (e.g. Allen et al. 2013; Clay et al. 2010). Early work on *Calluna* heath in Danish Jutland (Brown & Macfadyen 1969) proposed that soil CO_2 fluxes were controlled by the growth phase of the heather, which is closely related to canopy height. Brown and Macfadyen (1969) showed that mature (taller) heather had the greatest soil respiration rates while building phase (shorter) heather had the highest chlorophyll content and dry matter production. Work on a Swedish heath (Wallen 1987) showed that the percentage of assimilating biomass (relative to total above ground biomass) decreased with increasing stand age. Significantly more new adventitious shoots were recorded on younger (shorter) heather standards than on older (taller) stands indicating that post-burn heather regeneration is age, and thus height, limited (Kayll & Gimingham 1965).

In addition to the objective sense of using a physiological parameter like canopy height as a determinant of when to burn, its use is also desirable from a practical stand point. Heather canopy height is an easily measureable parameter in the field and thus land-managers will not have to rely on, potentially inaccurate, historic records of burning to decide when it is appropriate to burn their land. Furthermore, canopy height could perhaps be estimated by remote sensing with improved calibration of existing methods (e.g. Mehner et al. 2004; Yallop & Clutterbuck 2009).

Given the paucity of biogeochemical data on the matter, this study aims to investigate whether the CO_2 flux dynamics and balance of the ecosystem is related to the canopy height of heather on ombrotrophic peatlands. A potential outcome of this research is to identify whether canopy height is a simple but objective criterion for assessing when heather on blanket peat should be burned from a CO_2 exchange perspective. If canopy height proves to be a useful criterion, it is important to determine whether the suggested management height is in accord with that suggested from ecological and fire-risk management perspectives.

Sites and Methods

Field Sites

Data were gathered from a total of nine field sites (Table 1) distributed across three localities in the South Pennines (Keighley Moor – KM) and Peak District National Park (Bleaklow Plateau – BP and Goyt Valley – GV) of northern England (Fig. 1) where heather dominated on blanket peat. Average rainfall in the upland areas studied exceeds 1000 mm a^{-1} with an average annual air temperature (2007-2011, measured at a meteorological station on Bleaklow Plateau at 53°44’ N, 1°84’ E) of 6.8 ± 0.5 °C at 520 m above sea level.

Each site used in this study was instrumented with at least six plots. Each plot was instrumented in the same fashion with a uPVC dip-well, installed to one metre depth, for access to the water table and a 15 cm diameter uPVC gas collar for collecting CO_2 flux data. The gas collars were installed to a maximum depth of 5 cm, a depth which was intended to minimise root disturbance due to collar insertion (see Wang et al. 2005). On each plot of each site the vegetation present within each gas collar was recorded during the first monthly campaign. When *C. vulgaris* was present within the collar the height of the canopy (from soil surface to canopy top) was measured. All the sites, whether heather was present in all the collars or not, were installed entirely in areas dominated by heather, with the plots of any given site all sampling heather of the same age.

Field Methods

Data were gathered monthly for this work between July 2007 and February 2010. During this window any plots undergoing active monitoring were visited once a month (unless snow cover prevented access) at which point CO_2 flux, environmental and water table depth data would be recorded. The length of the measurement record differed between sites and localities, but each site has a time series of at least 12 calendar months (not necessarily coincident with the calendar year). Table 1 summarises the characteristics and length of record for each site and locality.

Carbon dioxide fluxes were measured with an infra-red gas analyser (EGM-4, PP-Systems, Hitchin, UK) with a clear 20 cm tall (total height above soil 30 cm when placed on collar), 15 cm diameter acrylic closed chamber (CPY-2, PP-Systems, Hitchin, UK) to measure fluxes of CO_2 from the permanently installed uPVC gas collars. Heather taller than the internal height of the chamber and collar was carefully manipulated so that the plant would fit into the chamber without damaging it; this limited the maximum canopy height which could be measured to less than 40 cm. All gas collars were left unmonitored for one month after insertion prior to any CO_2 flux to measurements. The protocols employed in the measurement of CO_2 fluxes were in line with previous research in the area (e.g. Clay et al. 2012; Rowson et al. 2010; Worrall et al. 2011). Ecosystem respiration (R_{eco}) fluxes were measured by covering the CPY-2 chamber with a tightly fitting uPVC sleeve that blocked all photosynthetically active radiation (PAR) from entering the chamber. Net ecosystem exchange (NEE) fluxes were measured using the CPY-2 chamber without the uPVC sleeve, i.e. with full sunlight entering the chamber. It was not possible with this method to measure gross photosynthesis (P_g) directly so it was estimated as the residual of the R_{eco} and NEE fluxes. While CO_2 fluxes were being measured PAR (µmol m^{-2} s^{-1}) and air temperature (K) probes were in operation within the chamber. The chamber was sealed to the gas collar by a tapering metal skirt so as to prevent interaction of chamber and ambient air during measurement. The air within the chamber was agitated by a 12 V fan to keep it well mixed and prevent stratification. Fluxes of CO_2 were measured over two minute intervals, after a set equilibration period, and CO_2 concentration data were recorded at a sampling interval of four seconds. Fluxes of CO_2 were calculated by taking the gradient of the linear regression of chamber CO_2 concentration with time and have been reported in units of g CO_2 m^{-2} h^{-1}. The sign convention used in this study is that CO_2 fluxes are considered relative to the atmospheric pool (i.e. P_g is negative and R_{eco} is positive). The depth of the water table relative to the peat surface was measured alongside CO_2 fluxes using a conductivity probe inserted into the dipwell adjacent to the gas collar.

Dataset Derivation

The overall dataset was sorted by vegetation type and a new dataset was subsetted from only the plots that contained heather within their gas collars. An important effect of compiling a dataset in this manner is that it leads to poor replication at the site level (i.e. not every plot on a given site will necessarily have heather in the gas collar). A benefit of this dataset is that most of the sites have been subject to the same land-management regime through managed rotational burning. Only one site (Ben – Table 1) is subject to a different management regime through vegetation cutting. Table 1 shows the number of replicates per canopy height window and land management practice (i.e. treatment).

Data Analysis

Quality control measures were undertaken on all CO_2 data by discounting any data outside 3σ of the mean. The total amount of data discounted by this method is given in Table 1 and never exceeded 3.27% of the whole dataset. Alongside this any CO_2 flux data inconsistent with the sign convention were checked and when appropriate discounted. In the case of P_g, 23.7% of the data were discounted because of incompatibility with the sign convention. This incompatibility happened because NEE had a greater positive magnitude than R_{eco} on these occasions. Eight percent of the R_{eco} data were discounted because of incompatibility with the sign convention. A summary of the data removed during the quality control stages is given in Table 1.

To address the proposition that fluxes of CO_2 from heather dominated blanket peatlands are related to the canopy height of heather, models including and excluding canopy height as a predictor were fitted to the data. The best fitting, most parsimonious model was selected using three criteria; the adjusted coefficient of determination (R^2 (adj)), root mean square error (RMSE) and the corrected Akaike Information Criterion (AICc). A well-fitting model will have a high R^2 (adj) and minimised RMSE and AICc scores.

Ecosystem respiration fluxes were modelled in three ways. Firstly, a well-known Arrhenius-type temperature-dependent model (Eq. 1) published by Lloyd and Taylor (1994) was fitted to the data.

Secondly, a multiple-linear regression (MLR) model was fitted to the data without using canopy height as a predictor (Eq. 2) and finally the same model was refitted with the addition of canopy height as a predictor (Eq. 3). Variance inflation factors (VIFs) for each predictor in the MLR models were calculated and any predictor with a VIF greater than five was excluded from the model. Moreover, any predictor with a $p > 0.05$ was also excluded from the model. Both the R_{eco} and $\ln(R_{eco})$ data were significantly non-normal ($p < 0.005$ for both). To minimise the departure from normality the response variable used in all models was $\ln(R_{eco})$ as the distribution of this dataset had the smallest Anderson-Darling (AD) statistic; AD $\ln(R_{eco}) = 1.90$ compared to AD $R_{eco} = 25.66$.

$$\ln(R_{eco}) = \ln(R_{10}) + E_0\left(\frac{1}{56.02} - \frac{1}{AT - 227.13}\right) \quad \textbf{(1)}$$

$$\ln(R_{eco}) = \frac{a}{AT} + bWTD + ccos\left(\frac{M\pi}{6}\right) + dsin\left(\frac{M\pi}{6}\right) + \mathrm{K} \quad \textbf{(2)}$$

$$\ln(R_{eco}) = \frac{a}{AT} + bWTD + ccos\left(\frac{M\pi}{6}\right) + dsin\left(\frac{M\pi}{6}\right) + eCH + \mathrm{K} \quad \textbf{(3)}$$

Where; R_{10} = ecosystem respiration at 10°C (estimated by linear regression); E_o = temperature sensitivity coefficient fitted by non-linear regression; AT = air temperature (K); WTD = water table depth (cm); M = month number; a, b, c, d, e = coefficients fitted by MLR; K = a constant fitted by MLR; and, CH = canopy height (cm).

Gross photosynthesis was also modelled in three ways. Firstly, a PAR-dependent rectangular hyperbola model (Thornley & Johnson 1990 - Eq. 4) was fitted by non-linear regression to the data. Then a MLR model without canopy height was fitted (Eq. 5) followed by a MLR model with canopy height (Eq. 6). Any predictor with a VIF greater than five was excluded from the model. Predictors with a $p > 0.05$ were also excluded. Both the P_g and $\ln(+P_g)$ data were significantly non-normal ($p < 0.005$ for both). To minimise the departure from normality, the response variable used in all models was $\ln(+P_g)$ as the distribution of this dataset had the smallest Anderson-Darling (AD) statistic; AD $\ln(+P_g) = 1.22$ compared to AD P_g = 28.75. ln(+Pg) is defined in Eq. 7 and is simply the natural log P_g with a positive sign (to avoid the problems of taking the logarithm of negative numbers).

$$\ln(+P_g) = \ln\left(\frac{P_{g(max)}\alpha PAR}{\alpha PAR + P_{g(max)}}\right) \quad \textbf{(4)}$$

$$\ln(+P_g) = \frac{a}{AT} + bWTD + cPAR + d\cos\left(\frac{M\pi}{6}\right) + e\sin\left(\frac{M\pi}{6}\right) + K \quad \textbf{(5)}$$

$$\ln(+P_g) = \frac{a}{AT} + bWTD + cPAR + d\cos\left(\frac{M\pi}{6}\right) + e\sin\left(\frac{M\pi}{6}\right) + fCH + K \quad \textbf{(6)}$$

$$\ln(+P_g) = \ln(P_g \times -1) \quad \textbf{(7)}$$

Where; $P_{g(max)}$ = the mean of P_g flux observations where PAR is > 1000 μmol m^{-2} s^{-1}; α = apparent quantum yield (the initial slope of the rectangular hyperbola) fitted by non-linear regression; PAR = photosynthetically active radiation (μmol m^{-2} s^{-1}); a, b, c, d, e, f = coefficients fitted by MLR; and, K = a constant fitted by MLR.

Using the best-fitting models of R_{eco} and P_g (including canopy height) an estimate of the annual net CO_2 budget of an upland blanket bog dominated by heather of varying canopy height (1 – 40 cm) was produced. This model was calculated using data taken from the meteorological station on Bleaklow Plateau. A CO_2 budget was calculated for the years 2010, 2011 and 2012.

Results

Ecosystem Respiration

Of the three models fitted to the ln(R_{eco}) data the Lloyd and Taylor (1994) model (Eq. 1) was the least well fitting, with an R^2 (adj) of 38.6% for the whole dataset (Fig. 2, Table 2). The RMSEs and AICc scores were the highest of all three models tested, whether or not the model was fitted to the whole dataset or to the datasets from each locality (Table 2). Examination of the standardized residuals by month revealed that the Lloyd and Taylor (1994) model generally overestimated respiration and that this overestimation was most apparent in winter/spring (December to May – Fig. 3a).

All MLR models performed better than the Lloyd and Taylor (1994) model, having larger R^2 (adj), lower RMSEs and lower AICc scores (Fig. 2, Table 2). The R^2 (adj) for Eq.2 (MLR without canopy height) was 48.2% for the whole dataset (Table 2). Eq. 2 did not perform as well as Eq. 3 (MLR with canopy height) whose R^2 (adj) was 50.3%, moreover, on all occasions Eq. 3 had the lowest overall AICc score. The monthly distribution of the standardized residuals for the MLR models (Eq. 2 and 3) were very similar, with no clear seasonal pattern to periods of over/under estimates (Fig. 3). When modelled on a locality-by-locality basis no significant relationship between $\ln(R_{eco})$ and canopy height was apparent on KM (Table 2). This may be because the range of canopy heights sampled on KM was smaller (Table 1) than the ranges sampled on BP and GV and thus KM alone is not representative. A significant relationship between $\ln(R_{eco})$ and canopy height was apparent on BP, GV and in the whole dataset (Table 2). The regression coefficients between $\ln(R_{eco})$ and canopy height were 0.0139 ± 0.0030, 0.0228 ± 0.0075 and 0.0154 ± 0.0038 $\Delta F\ cm^{-1}$ (where F is CO_2 flux in g $CO_2\ m^{-2}\ h^{-1}$) for the whole data set, BP and GV respectively. The sign of the regression coefficient always indicated a positive relationship between $\ln(R_{eco})$ and canopy height.

Gross Photosynthesis

When fitted to the whole dataset the Thornley and Johnson (1990) model (Eq. 4) was the least well-fitting, with an R^2 (adj) of 11.1% (Fig. 2, Table 3). The RMSEs and AICc scores were higher than either MLR model (Eq. 5 or 6 – Table 3).

All but one of the MLR models (whole dataset or by locality) had an R^2 (adj) greater than the Thornley and Johnson (1990) model. The exception was the Eq. 5 MLR (without canopy height) model for KM which had a lower R^2 (adj) than the Thornley and Johnson (1990) model. Nonetheless, all of the MLR (without canopy height) models had lower RSME and AICc scores than the comparable Thornley and Johnson (1990) models (Fig 2, Table 3). Overall the best fitting model was the Eq. 6 MLR (with canopy height) model which had the highest R^2 (adj) and lowest AICc and RSME values. Examination of the monthly sum of standard residuals by model (Fig. 3b) suggests that all models overestimated P_g in December and the first six months of the year and then underestimated P_g by a similar magnitude in the remaining five months of the year. When modelled on a locality-by-locality basis no significant relationship between $\ln(+P_g)$ and canopy height was identified on BP (Table 3). This is likely to be because the canopy heights sampled on BP were bimodal (5 – 10 cm and 33 – 36 cm), missing middling (most productive) canopy heights and thus BP alone is not representative. A significant relationship was nonetheless apparent for the whole data set, GV and KM (Table 3). The regression coefficients between canopy height and $\ln(+P_g)$ were -0.0318 ± 0.0050, -0.0326 ± 0.0057 and -0.0530 ± 0.0139 ΔF cm^{--1} for the whole dataset, GV and KM respectively. The sign of the regression coefficient always indicated a negative relationship between $\ln(+P_g)$ and canopy height.

Flux Balance and Annual CO_2 Budgets

It has been seen above that there are significant relationships between heather canopy height and both gross fluxes of CO_2 (R_{eco} and P_g). Examination of the ratio P_g/R_{eco} in the raw data (i.e. day time only data) suggests that the amount of photosynthesis per unit respiration decreases with increasing canopy height in an exponential fashion (Fig. 4). This agrees with the correlations identified in the output of the Eq.3 and Eq.6 (MLR with canopy height) models, suggesting that productivity will decrease as a heather stand ages and grows taller. To estimate NEE, the best fit models of the gross fluxes (i.e. the MLR models with canopy height) were used to predict NEE over 3 years (2010, 2011 and 2012). Net ecosystem exchange was estimated as the sum of daily R_{eco} and daily P_g over the time period. Fig. 5 shows the output of the daily NEE models for the years 2010 – 2012 for heather canopy heights of 1, 10, 20, 30 and 40 cm. It can be seen that, with a few exceptions for 1 cm, all canopy heights have positive NEE values (i.e. a net source) across the year with a minima in winter and a maxima in June/July. Given the decreasing amount of P_g and increasing amount of R_{eco} with an increasing canopy height, it can be seen that the largest net sources of CO_2 predicted occur under the 40 cm tall heather canopies.

Discussion

The principal aim of this study was to determine whether the point at which to reset the heather growth cycle can be predicted based upon canopy height, from a CO_2 flux perspective. The first stage of addressing this aim was to assess whether there is a relationship between CO_2 flux and canopy height. The results of this study showed that both R_{eco} and P_g are better predicted by models including a dependency on canopy height than models made up solely of hydro-meteorological predictors. Moreover, there was a significant decrease in the amount of photosynthesis per unit respiration with increasing canopy height (Fig. 4). Such a finding can be explained with reference to the growth cycle of heather, where shorter, juvenile/building heather has a greater amount of assimilating biomass per unit total above ground biomass than taller, mature/degenerate heather (Wallen 1987). Alongside this, shorter heather canopies, associated with earlier life cycle phases produce significantly less litter (~57 kg/ha for juvenile to between 162 – 433 kg/ha for degenerate; Cormack & Gimingham 1964) and thus provide less substrates for heterotrophic respiration per unit area than taller canopies. As a result of the increased amount of woody material and litter with increasing canopy height, clear positive relationships between fine- and coarse-fuel biomass and canopy height were observed by Davies et al.

(2008) for Scottish heather communities. This underlines the wildfire risk of taller heather canopies. Wildfire on peatlands can completely de-vegetate large areas of ground and has resulted in massive losses of carbon to the environment on Bleaklow Plateau (e.g. Evans et al. 2006; Worrall et al. 2011). Thus it could be argued that burning based on canopy height intended to minimise wildfire risk is justified from a biogeochemical perspective also, given the potential consequences of wildfire for peatland carbon stores. However, this would only be an indirect recommendation, not based on the outcomes of this study.

The second stage of addressing the principal aim of this study was to determine whether the relationships between canopy height and CO_2 flux indicate a point at which the heather should be managed. The ecological studies of Burch (2008) and Harris et al. (2011) recommend a canopy height for burning of between 25 – 30 cm in order to maximise bryophyte (particularly *Sphagnum* spp.) dominance and diversity. From a CO_2 flux perspective the most appropriate indicator of when to manage heather on blanket peat would be the transition from a net sink to a net source of CO_2. However, annual modelling of net CO_2 flux, based on the best fit models from this dataset, predicted that at no canopy height would the heathlands be a net annual sink of CO_2 based on the prevailing conditions measured at the Bleaklow Plateau weather station between the years 2010 - 2012. This is not necessarily a surprise as areas of blanket peat dominated by heather were also found to have positive NEE in a study of CO_2 flux dynamics on the Atlantic coast of Ireland (Laine et al. 2007). Laine et al. (2007) attribute this finding to the fact that the heather dominated areas of the bog had the deepest water levels. They found that deeper water tables enhanced R_{eco} relative to the wetter areas of the same bog. Mean water tables for the localities on which this study created models were; 55.6 ± 0.73, 30.0 ± 0.89 and 12.9 ± 0.94 cm for BP, GV and KM respectively which are all drier than or comparable to the driest areas in Laine et al. (2007). Moreover, the mean water table depth used for prediction (from the Bleaklow weather station) is 58.7 ± 0.07 cm. As such, it is likely that R_{eco} has been enhanced by the dry conditions of the sites examined in this study and that this leads the heather dominated bogs in these areas to be perpetual net sources of CO_2 to the environment.

The fact that there is no predicted transition between sink and source means that canopy height cannot be used as a direct indicator of when to manage heather, on the bogs studied. What can be demonstrated, however, is that as the heather grows taller the rate of net CO_2 loss increases. Thus, shorter canopy heights should be preferred over taller canopies from this perspective (i.e. not allowing canopy heights to get very tall represents an avoided loss of CO_2). Moreover, there is nothing in the analysis herein that would disagree with the recommendations of Burch (2008) and Harris et al. (2011) to manage the heather around 25 cm canopy height. Indeed, it can be seen on Fig. 4 that the ratio of P_g to day time R_{eco} decreases exponentially with increasing canopy height and that most of the data with a ratio greater than 1 in the day time is of a canopy height less than 25 cm.

The fact that no sink to source transition was identified in this context does not imply the same result in all contexts. It is argued here that the relative dryness of the bogs examined enhanced R_{eco}; on wetter sites it may well be possible to use canopy height as a proxy for the transition between net sink to source of CO_2. That said, the reasoning for using canopy height as a predictor of when to manage heather was to allow for broadly applicable recommendations of when to manage to be made. While there is a relationship between CO_2 flux and heather canopy height, it will be modified by site specific conditions and thus, in the same way as for rotational intervals, it is not possible to draw broadly applicable recommendations on this basis.

The finding that blanket bogs dominated by heather, of any canopy height, are likely to be net CO_2 sources in South Pennine/Peak District areas is important. The blanket bogs of the Peak District National Park are climatically marginal and were found by Clark et al. (2010) to be the third most vulnerable in the UK to climate change induced reductions in available bioclimatic space for blanket bog formation. Therefore, this problem is likely to get worse in the coming decades. Moreover, DOC concentrations were found by Armstrong et al. (2012) to be higher under heather than either *Sphagnum* spp. or sedges (e.g. *Eriophorum* spp.) and they recommend upland vegetation management away from heather dominance for this reason. The results of this study would tend to support their views, but from the perspective CO_2 fluxes. Such a transition, however, would need to be carefully managed. Reed et al. (2013) suggest that a programme of extensification with reduced levels of heather burning may well lead to an increasing wildfire risk in the uplands, as the heather stands grow older and become degenerate. They recommend extensification focused on areas that would lead to restoration of degraded peatlands. Moreover, Armstrong et al. (2012) suggest that active measures such as artificial *Sphagnum* spp. propagation (e.g. Hinde et al. 2010) and hydrological interventions (Allott et al. 2009; Dixon et al. 2014) would be desirable to increase surface wetness and decrease heather dominance. Such schemes appear to be working towards restoring the biogeochemical functioning of cut-over Canadian bogs (e.g. Waddington et al. 2010) and may hold the key to protecting and restoring at risk UK blanket peat. However, as heathlands are such important landscapes culturally, aesthetically and economically, management away from heather is only recommended on the most vulnerable blanket bogs.

Conclusions

There are three conclusions to this study. Firstly, both gross CO_2 fluxes from blanket peat dominated by heather are controlled, in part, by heather canopy height. Shorter, younger heather has a greater amount of photosynthesis per unit respiration than older, taller heather. Secondly, despite this control it was not possible to infer a broadly applicable recommendation of when to manage heather based upon canopy height alone. This was because all heather canopy heights were modelled to be net sources of

CO_2 under the conditions prevalent at the Bleaklow weather station and as such, no sink to source transition was observed for CO_2. Nonetheless, it is clear that as heather becomes taller the net amount of CO_2 the ecosystem releases increases. Finally, the fact that blanket peat dominated by heather is a net CO_2 source suggests that heather may be injurious to peatland growth in climatically marginal areas like these and, as such, vegetation management towards a more biogeochemically appropriate community is recommended to enhance resilience to climate change.

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Tables and Figures

Table 1 – Summary of Locality, Site and Dataset Characteristics

Locality	Site	Plots	*C. vulgaris* height range (cm)	Altitude (m a.s.l.)	Management	Time series	N (R_{eco})	N (NEE)	N (P_g)
BP	WM	2	5 - 10	468	Burning	07/2007 - 02/2009	25	20	16
	WR	5	33 - 36	468	Burning	07/2007 - 03/2009	69	75	54
GV	Ben	2	4 - 5	430	Cutting	06/2008 - 01/2010	26	26	22
	Bottle	5	4 - 10	432-442	Burning	07/2008 - 01/2010	77	75	67
	RL	2	22 - 28	435-441	Burning	06/2008 - 01/2010	33	32	25
	OB	5	5 - 7	430	Burning	06/2008 - 01/2010	79	75	58
	Prom	4	32 - 37	456	Burning	06/2008 - 01/2010	69	66	48
KM	BA	7	16 - 28	396-417	Burning	03/2009 - 02/2010	66	57	44
	BB	7	5 - 6	412-425	Burning	03/2009 - 02/2010	62	64	51
					Quality Control	Used (3σ and incorrect sign removed)	506	490	385
						After Incorrect sign removed	517	505	398
						Total	550	505	505

Table 2 – Summary of $\ln(R_{eco})$ model results

Locality	**Eq. 1 - Lloyd and Taylor (1994)**			
	n	R^2 (adj)	RMSE	AICc
All	506	38.6%	1.12	-21.71
BP	94	40.1%	1.23	15.99
GV	284	36.3%	1.17	21.90
KM	128	50.7%	0.78	-97.03

Locality	**Eq. 2 - MLR (no CH)**			
	n	R^2 (adj)	RMSE	AICc
All	506	48.2%	0.91	-227.24
BP	94	42.7%	1.05	-11.29
GV	284	46.9%	0.94	-100.02
KM	128	64.2%	0.61	-154.76

Locality	**Eq. 3 - MLR (CH)**			
	n	R^2 (adj)	RMSE	AICc
All	506	50.3%	0.89	-246.11
BP	94	47.6%	0.99	-17.97
GV	284	49.7%	0.91	-113.90
KM	128	-	-	-

Table 3 – Summary of $\ln(+P_g)$ model results

Locality	Eq. 4 - Thornley & Johnson (1990)			
	n	R^2 (adj)	RMSE	AICc
All	385	11.1%	1.30	208.35
BP	70	20.8%	1.27	37.14
GV	220	9.6%	1.33	128.41
KM	95	16.7%	1.71	105.78
Locality	**Eq. 5 - MLR (no CH)**			
	n	R^2 (adj)	RMSE	AICc
All	385	18.0%	1.17	123.91
BP	70	36.4%	0.97	1.85
GV	220	29.4%	1.09	45.15
KM	95	10.8%	1.22	42.09
Locality	**Eq. 6 - MLR (CH)**			
	n	R^2 (adj)	RMSE	AICc
All	385	25.6%	1.11	87.15
BP	70	-	-	-
GV	220	37.9%	1.01	15.96
KM	95	22.3%	1.13	30.08

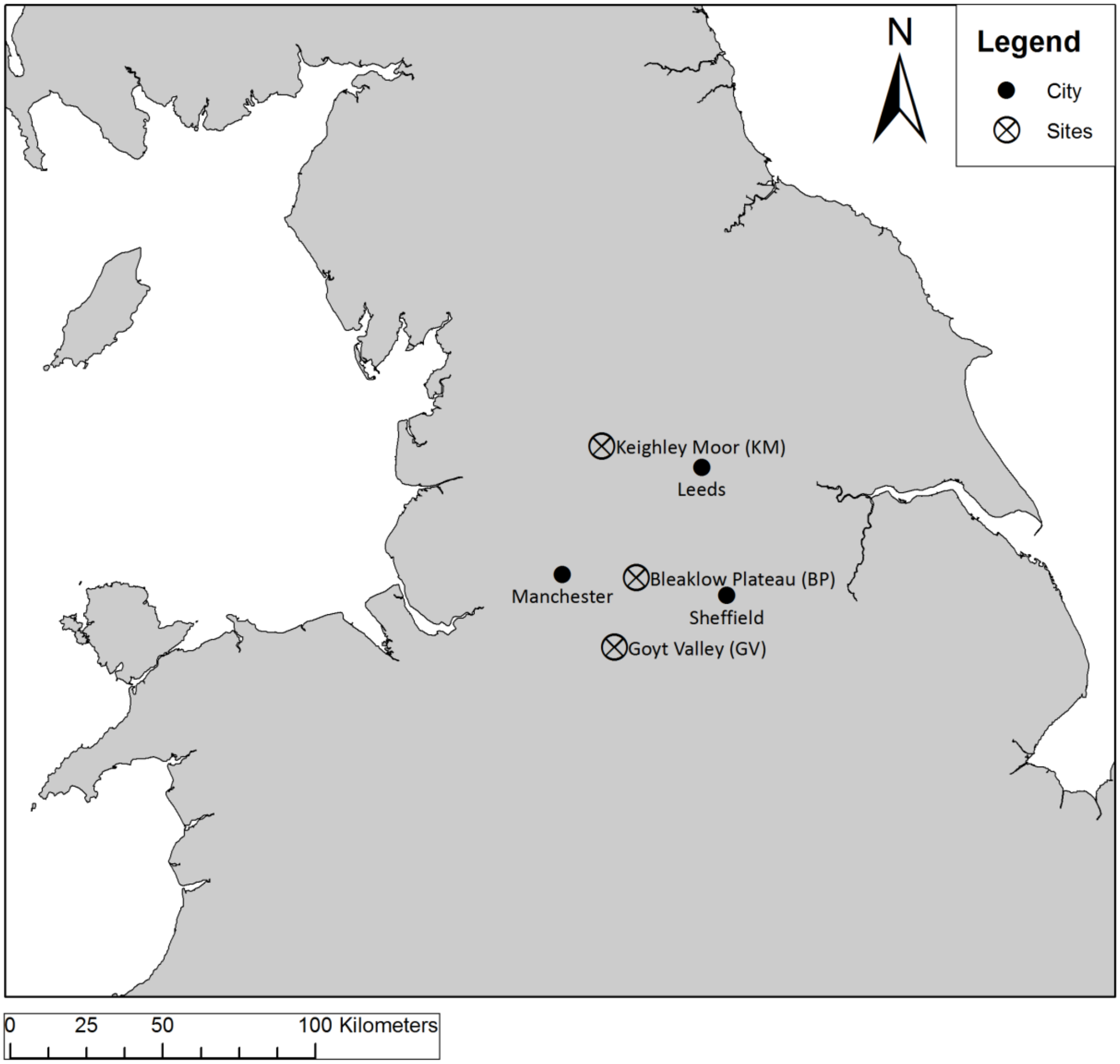

Fig. 1 – Map of northern England showing the distribution of the three localities in relation to the closest major urban centres.

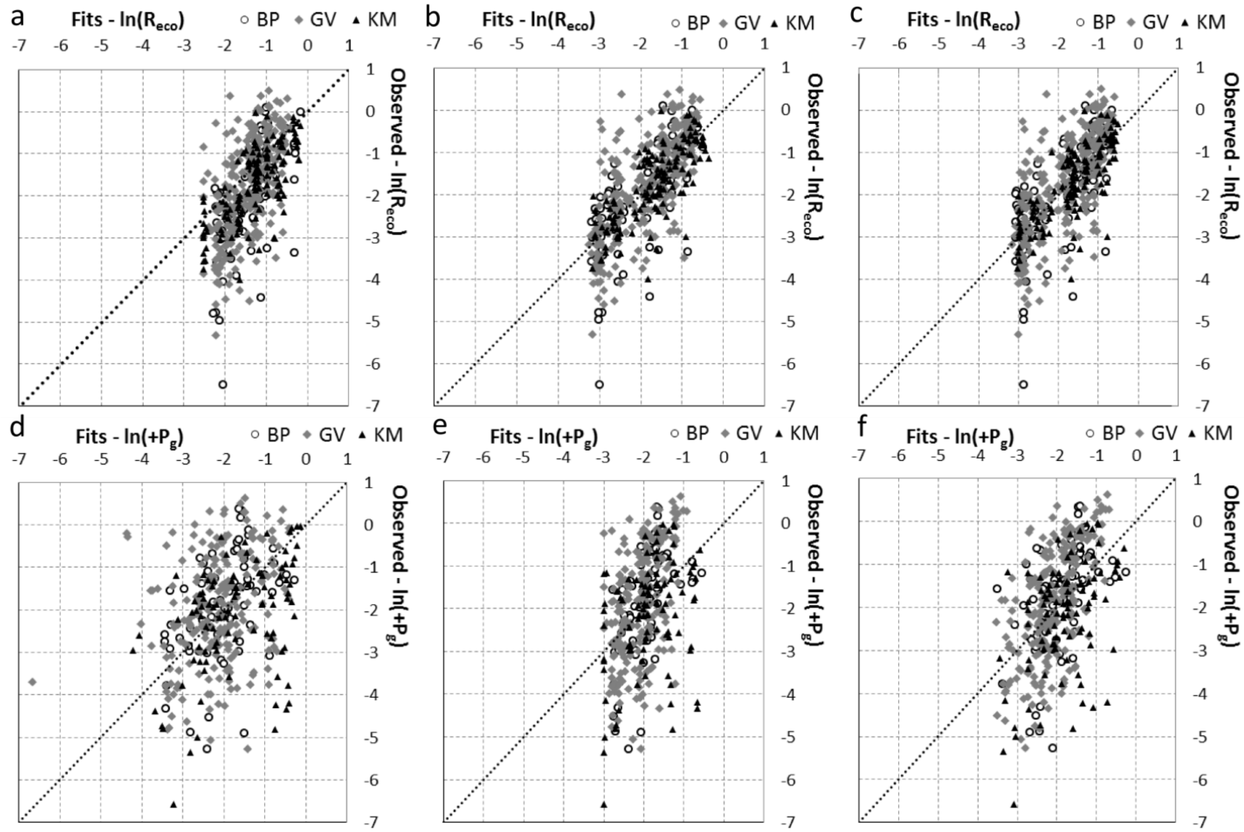

Fig. 2 – Model fits versus observed values by locality. Panels a – c are for Eqs. 1 – 3 (ecosystem respiration models) respectively. Panels d – f are for Eqs. 4 – 6 (photosynthesis models) respectively.

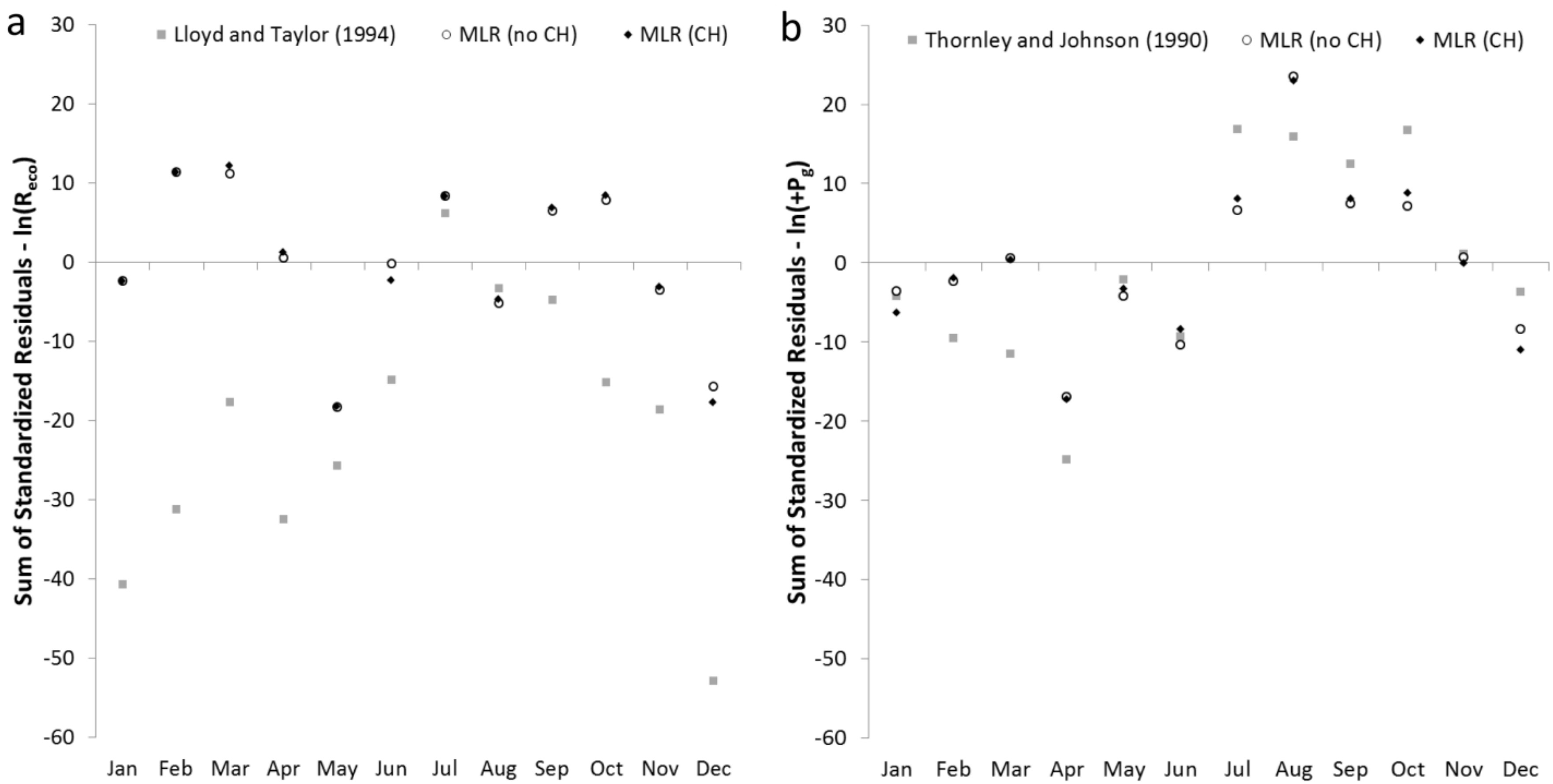

Fig. 3 – Sum of standardized residuals by model (see key) and by month (x-axis) for (a) ln(R_{eco}) and (b) ln(+P_g) fitted to the whole dataset.

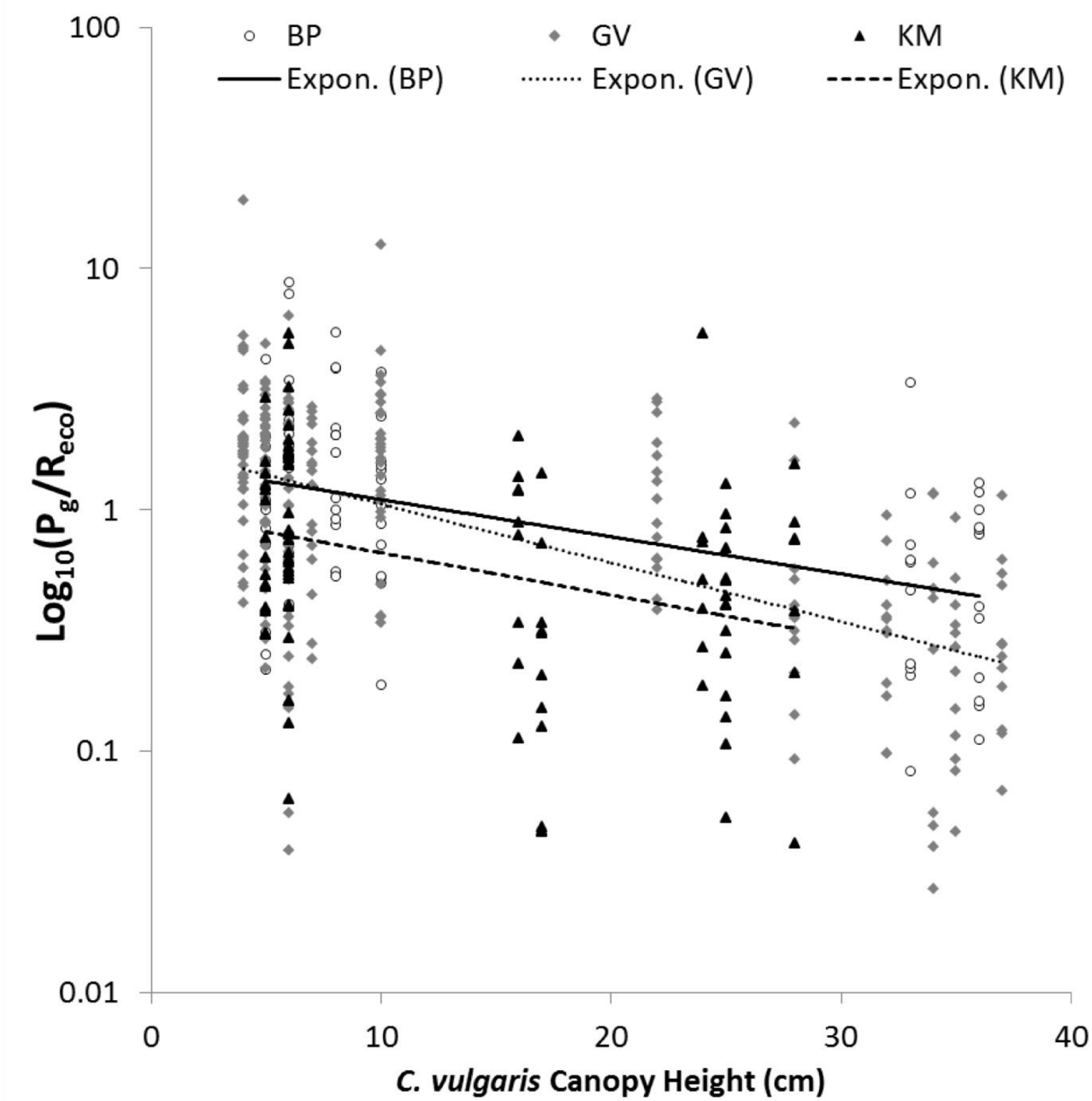

Fig. 4 – The relationship between; P_g/R_{eco} and *C. vulgaris* canopy height (cm), by site. Exponential trend lines were fitted for each dataset for each site; note that these trend lines appear linear due to the log-normal axes.

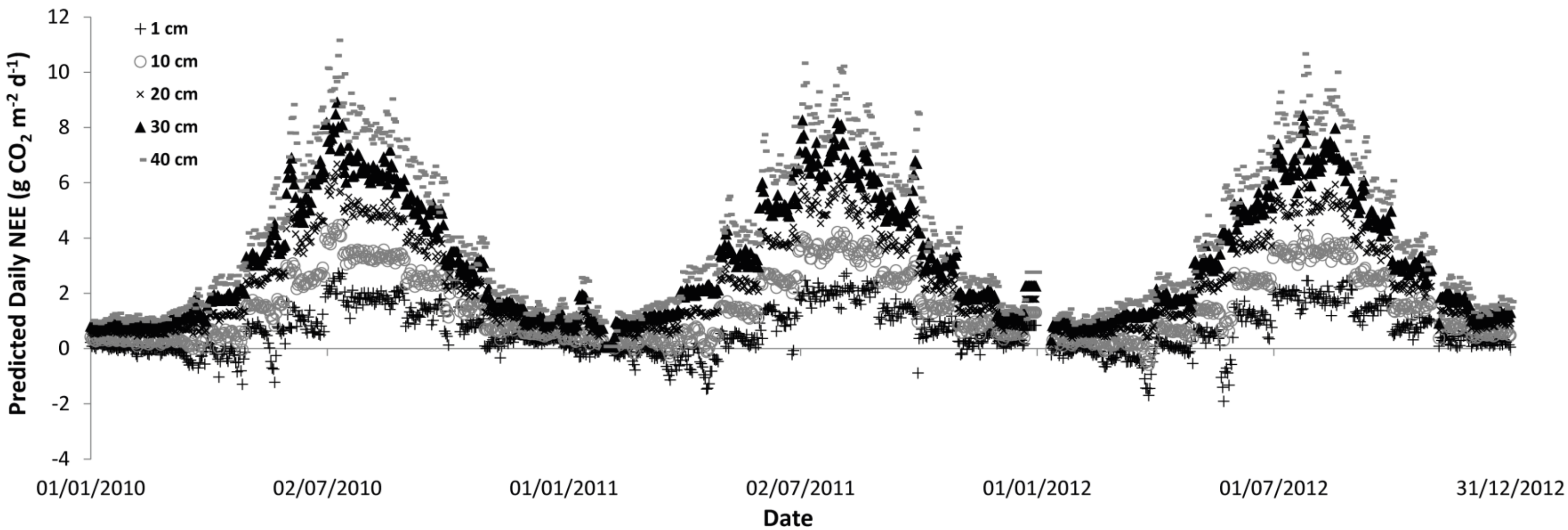

Fig. 5 – Predicted NEE calculated for canopy heights between 1 and 40 cm based Eq.'s 3 and 6 powered by hydro-meteorological data from the Bleaklow Plateau weather station (01/01/2010 – 31/12/2012).